ORIGINS OF SOUTHERN HEMISPHERE ENDEMISM, ESPECIALLY AMONG MARINE CRUSTACEA

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There are a number of hypotheses to explain the high endemism above the species level in the Southern Hemisphere. The separation of Gondwana from Laurasia by the Tethys Sea during the Mesozoic and the subsequent breakup of Gondwanaland evidently explains some of the terrestrial and freshwater endemism. Marine endemism is not generally explained by these events however, but rather by late Mesozoic and Tertiary reliction of tropical forms, or by extinction of Northern Hemisphere portions of amphitropical forms. Amphitropicality apparently can result from dispersal across the tropics. But it can also result from exclusion of an earlier biota from the tropics. Exclusion often involves replacement by more advanced forms concomitant, at least since the Miocene, with warming and compression of the tropics.

Areas of endemism in both hemispheres can be relatively localised and this provides insights into why a number of older taxa have survived there while going extinct elsewhere. Areas of marine endemism in the Southern Hemisphere are presently more evident in southeast Australia, Tasmania, and New Zealand than in other Southern Hemisphere outposts apparently because much of it has developed in the western Pacific since the breakup of Tethys. ☐ *Crustacea, Southern Hemisphere, endemism, Gondwana, Tethys, reliction, amphitropical, dispersal, vicariance.*

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There is a high degree of endemism in the Southern Hemisphere, compared to the Northern Hemisphere, on land and fresh water and, perhaps surprisingly, in the sea. While it is generally most pronounced in Australia, New Zealand, and islands of the southwest Pacific, some extends around the Southern Hemisphere, to oceanic islands as well as the southern parts of South America, Africa, and India.

No one hypothesis explains the situation, although the breakup of Gondwanaland, after its long separation from Laurasia by the Tethys Sea, is apparently the best explanation for many of the freshwater and terrestrial forms that are sufficiently old and lack propagules capable of long range, trans-oceanic dispersal. The marine situation is less clear since most forms have, or had, significant dispersal capabilities, and many of the Southern Hemisphere endemics are too young to have been part of Gondwanaland (McDowall, 1978; Newman, 1979). There is a growing consensus that much of the apparent endemism in the Southern Hemisphere is due to the extinction of Northern Hemisphere counterparts rather than its having evolved there (Eskov and Golovatch, 1986; Newman and Foster, 1987).

In the present paper some crustacean distributions will be examined for endemism, especially in the Southern Hemisphere. But before getting to them, a brief discussion of climatic change, the development of tropical provincialism following the breakup of Gondwanaland and Tethys, and examples and hypotheses relevant to the matter of Southern Hemisphere endemism, are in order. Some marine molluscs will be used as examples because, by and large, they have a good fossil record.

BREAKUP OF GONDWANA AND TETHYS, AND CONCOMITANT CLIMATIC CHANGE

It has long been recognised that the marine climate was equably warm up to relatively high latitudes in the late Mesozoic (Murray, 1896), but it is only in recent years that we have come to accept that in the Late Cretaceous, approximately 100 million years before present (MYBP), the super continent Pangea was being split into Laurasia and Gondwana with the tropical sea known as Tethys in between (Kennett, 1982; Windley, 1984). A Tethyan marine biota was not only distributed throughout this sea, it included a large pantropical element that circled the globe via oceanic currents and islands of Panthalassa, the present day Pacific (Hamilton, 1956).

With continued continental drift, the Atlantic began to open up and Gondwana to fragment. Both processes led to the breakup of Tethys and, hence, to the tropical provincialism we see today (Ekman, 1953). Significant events in the breakup of Tethys included the northward movement of Africa and its contact with Eurasia in the lower Miocene, about 18 MYBP, followed by the closure at Suez, virtually cutting off the tropical Indian Ocean from the Atlantic in the Middle Miocene, 12–14 MYBP (Kennett, 1982; Windley, 1984). Likewise, New Guinea-Australia moved north to contact southeast Asia, thereby diverting the North Equatorial Current from the Indian Ocean to the North Pacific in the Upper Miocene, approximately 7 MYBP (Kennett *et al.*, 1985). The Panamic closure separated the widening Atlantic from the tropical East Pacific in the Pliocene, (3.1-3.6 MYBP [Rosenblatt and Waples, 1986]).

With the onset of the Tertiary, the shallow equable seas of the Mesozoic began to cool and retreat, at low as well as high latitudes (Shackleton, 1984). This trend persisted throughout the Paleogene, about 25–30 MYBP. Then a new trend, correlating with the establishment of circum-Antarctic deep-water circulation near the end of the Oligocene, set in (Van Andel, 1979). It is noteworthy that, while the poles continued to cool, the tropical regime reversed and began to warm to the extent that for the most part, the tropics are warmer today than they were at the close of the Cretaceous (Shackleton, 1984). As will be discussed below, this warming phenomenon was used by Valentine (1984), in lieu of the biological factors of Théel (1911), in explaining amphitropical reliction via exclusion from the deep tropics. These two hypotheses stand in marked contrast to migration across the tropics, especially during the Pleistocene, utilised by Darwin (1859) in explaining amphitropicality.

HYPOTHESES RELEVANT TO SOUTHERN HEMISPHERE ENDEMISM

Five hypotheses relevant to the origin of Southern Hemisphere endemism are identified here, and they can be divided between three categories. The categorization is not intended to be precise; rather, it is simply to give us areas on which to focus. The hypotheses, listed here, are elaborated upon below:

I) Centres of origin.

II) Dispersal to the Southern Hemisphere followed by extinction in Northern Hemisphere (includes one form of amphitropicality, cf. III B, 2 below).

III) Vicariance: Relict and relic biotas[1]; involves two processes (A and B), the second and sometimes the first being followed by extinction in the Northern Hemisphere:

A. The breakup of Pangea and/or Gondwana.
B. The breakup of Tethys. Relicts and relics of Tethys fall into two principal types:
  1. Those resulting from division of the tropics.
  2. Those resulting from exclusion from the tropics (second form of amphitropicality).

I. CENTRE OF ORIGIN

The taxon in question evolved in the region where it is found (Fig. 1). Species can certainly be found at or near their place of origin, but the probability decreases with the age of the species, and that higher taxa evolved where they are presently found decreases dramatically with taxonomic rank. Therefore, a centre of origin hypothesis is risky unless one has an excellent stratigraphic record. The hypothesis can often be falsified by the discovery of a single fossil or living population in the 'wrong place' and therefore it should be proffered with caution. In order to emphasise this point, we can now look at some examples of molluscs that would have fallen under a centre of origin hypothesis had it not been for the fossil record.

Scattered populations of a gastropod, *Neritopsis radula*, range across the Indo-West Pacific, from islands off East Africa to the Hawaiian Archipelago. One might conclude that the present distribution includes the centre of origin. However, approximately 100 fossil species of *Neritopsis* are recognised and *N. radula*, the sole surviving member of the Neritopsidae, is itself known from the Eocene of the Paris Basin (Batten, 1984). Hence, it is a Tethyan relic at the familial as well as generic and specific levels; a relic par excellence.

Another Tethyan relic is the bivalve mollusc *Neotrigonia* represented by six extant species found around Australia. They are the last surviv-

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[1] A 'relict' population is one separated from a parent population by some vicariant event while a 'relic' population consists of the last survivors of an ancient radiation

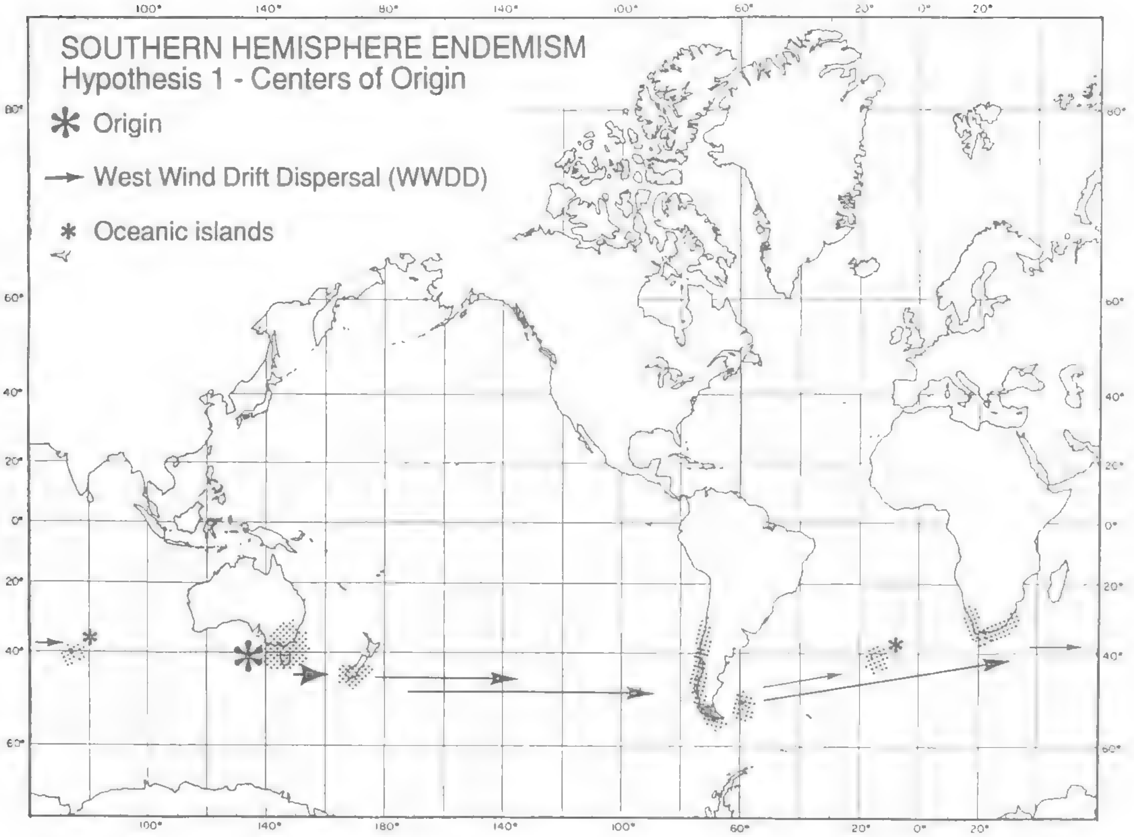

FIG. 1. Hypothesis 1 — Centre of Origin. The origin of a hypothetical Southern Hemisphere endemic has been arbitrarily placed in southeastern Australia (large asterisk). The taxon may subsequently disperse, in this example, via the West Wind Drift (Fell, 1962) to South America, South Africa etc. (arrows) and involving oceanic island stepping stones (small asterisks; stippling indicates presence of established populations). Presence on oceanic islands is evidence for post-Gondwanan long-range dispersal (Newman, 1979a). The hypothesis can be falsified by fossil evidence from other continental sediments of Gondwanan age, or by appropriate evidence from the Northern Hemisphere.

ing members of the Trigoniidae which became largely extinct at the end of the Cretaceous in the North Pacific and Europe (Stanley, 1984). Unlike the Indo-West Pacific Tethyan relic *Neritopsis*, *Neotrigonia* is a Southern Hemisphere endemic as well, by virtue of having gone extinct in the Northern Hemisphere. The commonness of this latter pattern is illustrated by the following three relic gastropod molluscs of the Southern Hemisphere: 1) *Campanile symbolicum* of southwestern Australia, the sole surviving species of the Campanilidae which flourished in Tethys of the early Tertiary (Houbrick, 1984a); 2) *Diastoma melanoides* of southern Australia, the sole surviving species of the Diastomatidae which flourished in the Eocene of Tethys (Houbrick, 1984b); and 3) *Gourmya gourmyi* of New Caledonia, New Hebrides, the Chesterfield Islands and Marion Reef of the Coral Sea, the sole surviving species of the genus which traces back to the Eocene of the Paris Basin, Tethys to the end of the Miocene, and the Pliocene of Japan (Houbrick, 1984c).

As well as emphasising the value of the fossil record, the foregoing gives some perspective. While the course of extinction that led to these Southern Hemisphere endemics apparently had its roots in the Paleogene, it apparently did not become highly restrictive until the Neogene. These examples demonstrate how readily a centre of origin hypothesis can be falsified (Eskov and Golovatch, 1986; Newman and Foster, 1987) and the issue will be taken up shortly concerning some crustaceans.

II. Dispersal to Southern Hemisphere

Immigration from the Northern to the Southern Hemisphere, with subsequent extinction in

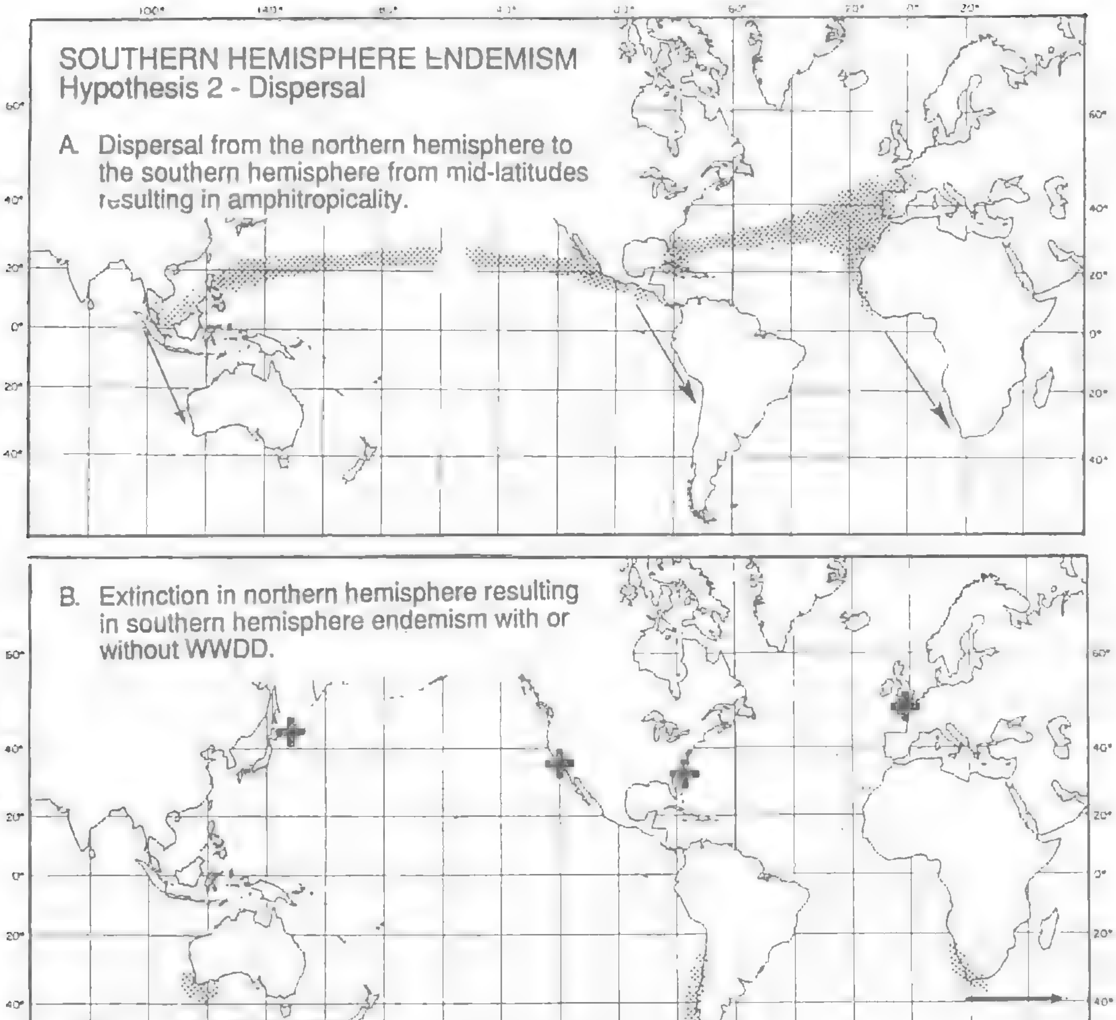

FIG. 2. Hypothesis 2 — Dispersal and Extinction. A, Dispersal of Northern Hemisphere propagules (stippled, planktonic or benthic) to the Southern Hemisphere, whereby the taxa involved become amphitropical (Darwin, 1859). Immigration is most easily accomplished where eastern boundary conditions exist (arrows), beneath a shallow thermocline and or during cool periods such as the Pleistocene. B, If Northern Hemisphere amphitropical counterparts of Southern Hemisphere immigrants go extinct (crosses), the immigrants become Southern Hemisphere endemics. Southern Hemisphere immigrants may disperse via the West Wind Drift (arrows). Evidence needed to falsify hypothesis 1 generally supports this and subsequent hypotheses to one extent or another.

the Northern Hemisphere, is a simple and straight forward way of explaining both amphitropicality and Southern Hemisphere endemics (Fig. 2). Migration during the Pleistocene, across the tropics, could have been by way of high mountains for terrestrial forms, or across equatorial waters for marine forms (Darwin, 1859). It is of course also possible to go beneath tropical waters, especially under eastern boundary conditions where the thermocline is shallow and upwelling prevails (Ekman, 1953; Hubbs, 1952).

The foregoing molluscan examples are not envisaged as falling into this category because they were apparently originally wide-ranging Tethyan populations. Thus it may be difficult to decide between this hypothesis and that covered under III B, 2 below, since both are two-step processes involving extinction in the Northern Hemisphere. But because the present hypothesis involves migration across the tropics rather than exclusion from the tropics in establishing amphitropicality, the distinction is important to our understanding.

III. VICARIANCE

Such hypotheses for the origin of Southern Hemisphere endemism involve two processes: A) the breakup of Pangea and Gondwanaland (Fig. 3); and, B) events included in and following the breakup of Tethys (Figs 4 and 5).

A., Relicts and relics of Gondwanaland seem to be limited primarily to terrestrial and freshwater biotas and examples among the freshwater crustaceans will be taken up shortly.

B., Tethyan relicts and relics (III B), on the other hand, include many marine forms. Two patterns can be identified and they need to be distinguished here. The first (Fig. 4) involves retreat of warm seas of the world, since the Cretaceous, towards centres of distribution. The second (Fig. 5) involves splitting of primarily Paleogene tropical populations into amphitropical populations beginning in the Oligocene (Kennett, 1982; Newman and Foster, 1987). Both processes may ultimately lead to hemispheric endemism, commonly in the Southern Hemisphere and especially in the southwestern Pacific.

AMPHITROPICAL DISTRIBUTIONS

Examples of molluscs given above (the bivalve, *Neotrigonia*, and the gastropods *Campanile*, *Diastoma*, and *Gourmya*) are all Southern Hemisphere endemics with Tethyan histories. They appear to be a subset of the Indo-West Pacific relict pattern, a pattern also observed at bathyal depths by Ameziane-Cominardi *et al.* (1987) and Richer de Forges (1990). However, these authors do not explore the possibility of their once having been amphitropical. Therefore we can move on to amphitropical distributions and their role in the origin of Southern Hemisphere endemism.

There are numerous examples of amphitropical distributions (cf. Good, 1964; Van Balgooy, 1971; Randall, 1981; Springer, 1982; Briggs, 1987a, b), and hypotheses regarding their origins were recently reviewed (Newman and Foster, 1987). There were two noted above deemed relevant to marine forms – that of Darwin (1859) involving migrations across the tropics especially during the Pleistocene (Fig. 4) and that of Théel (1911) and Valentine (1984) involving the splitting of a previously tropical biota into northern and southern populations (Fig. 5).

Darwin's (1859) hypothesis involved cooling during the glacial epochs whereby some terrestrial and marine plants and animals could have ranged across the tropics to become amphitropical when the cool period abated. This hypothesis has been popular with marine biogeographers studying fish and plankton, especially those working with plankton or under eastern boundary conditions such as along the shores of the tropical East Pacific, or elsewhere where upwelling occurs (Hubbs, 1952; Brinton, 1962; Van der Spoel and Heyman, 1983; Fleminger, 1986). Although the tropical East Pacific can become relatively warm during El Niño period (Ramage, 1986) it is generally cool compared to the same latitudes in the West Pacific due to prevailing currents from the north and especially the south, and the upwelling associated with them. From deep-sea drilling results, it is known that the belt was much narrower during the last glacial period, 18 000 YBP, than it is today (Moore *et al.*, 1980). Amphitropicality, established by migration across the tropics at such times, would then be followed by extinction, generally in the Northern Hemisphere whereby the Southern Hemisphere populations become endemic at some level.

On the other hand, Théel's (1911) hypothesis for the origin of amphitropicality concerns splitting of tropical populations; that is, peripheral reliction through replacement in the deep tropics by more advanced forms via competition. Valentine (1984) looks as well to the physiological impact of warming of the deep tropics noted above under climatic change[2]. These two hypotheses seem to go hand in hand since many modern forms (structurally more advanced and often known to be geologically younger) commonly dominate the deep tropics while some

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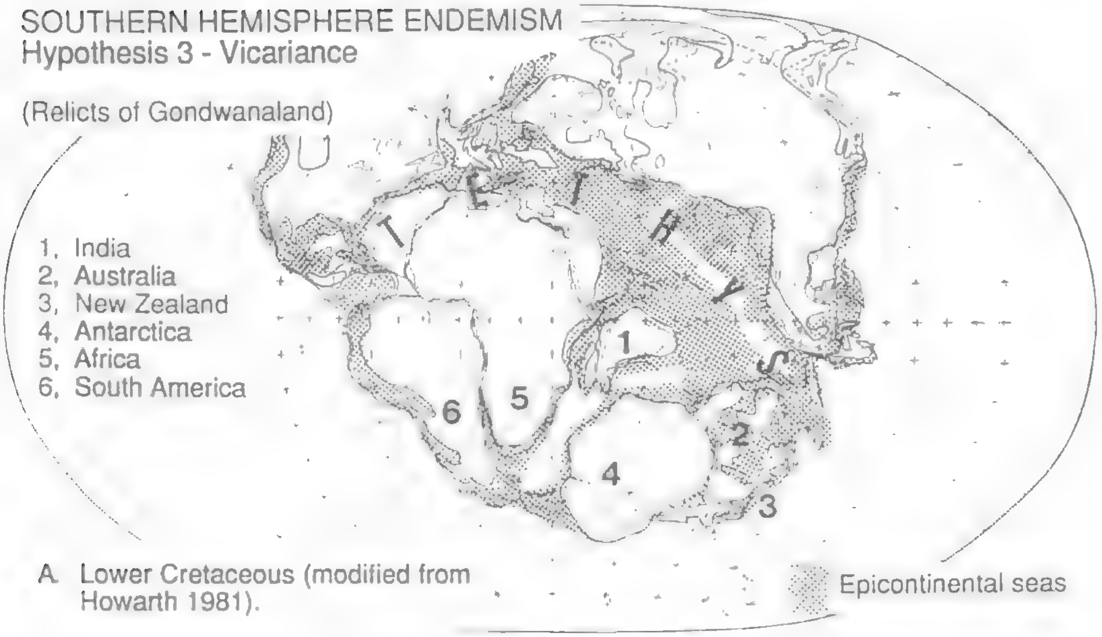
[2] Briggs (1987a) dismisses Shackleton's earlier temperature curves for high and low latitudes over the past 100 MY because of a difficulty with the method due to water tied up in glacial ice. However, he does not cite Shackleton (1984) where the difficulty is apparently taken into account.



A. Lower Cretaceous (modified from Howarth 1981).

B. Paleogene (modified from Adams 1981)

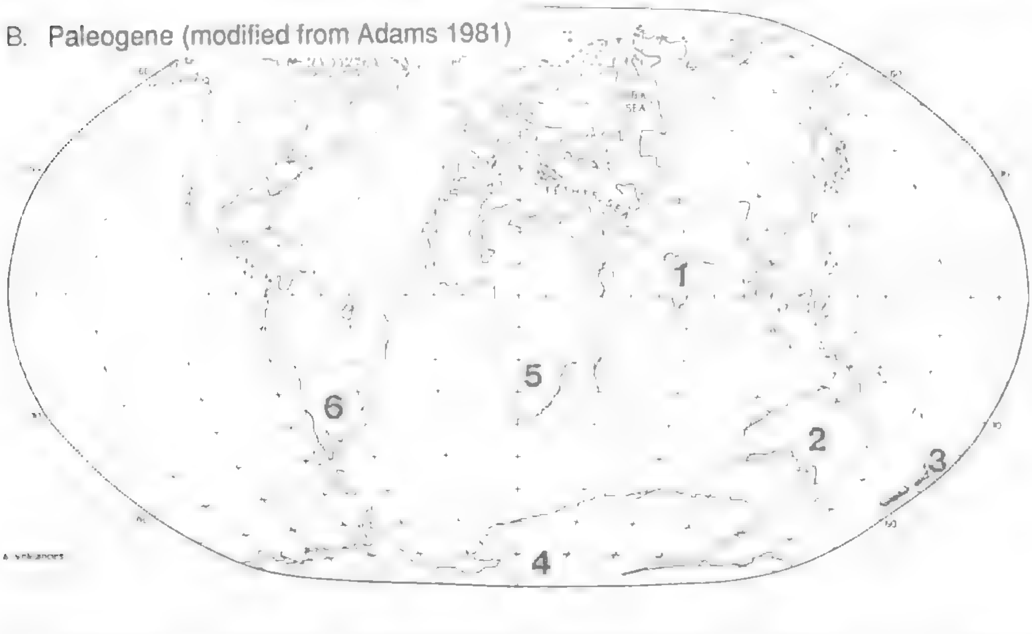


FIG. 3. Hypothesis 3 — Vicariance. Relicts and relics of Gondwanaland. A, Contiguity of the six Gondwanan continents and the extent of Tethyan and adjacent epicontinental seas (stippled, modified from Howarth, 1981). Tethys virtually separated Gondwana from Laurasia during the Mesozoic, up through the Cretaceous. During this time, tropical Tethys formed a significant barrier to dispersal between Laurasia and Gondwana for terrestrial and freshwater forms. On the other hand, cosmopolitan elements of the Tethyan marine biota girdled the earth during this period via currents and oceanic islands of Panthalassa (Hamilton, 1956). B, Positions of the six Gondwanan continents by the Palaeogene (modified from Adams, 1981). The breakup of Gondwanaland apparently explains the distribution of many terrestrial and freshwater forms endemic to the Southern Hemisphere.

older forms tend to be peripheral (Théel, 1911; Newman and Foster, 1987). Since temperature is presently apparently the primary factor in maintaining the separation between some amphitropical populations, the current hypothesis is classified as vicariant. It is instructive in this regard that in situations such as the East Pacific some populations have not been split completely (Ekman, 1953) and these have been termed 'paramphitropical'[3].

THE METHOD USED FOR ANALYSIS

The material covered in the foregoing introduction includes areas of historical geology and climatology as well as considerations of present day distributions of some marine molluscs having a significant fossil record. These data were integrated to varying degrees into hypotheses involving the origins of Southern Hemisphere endemism. This background can now be applied to the distribution patterns seen in a number of freshwater as well as marine crustaceans. The question is often whether the present distribution of a given taxon is more or less as far as the radiation reached, or is the result of reliction of a once much wider pattern. Obviously to have been wide ranging, a taxon would have to have radiated at one time or another, but the place of origin and the direction of the radiation are usually lost in antiquity. Likewise, the course of a subsequent reliction is also often difficult if not impossible to document.

Distributions are plotted where appropriate, and inspected for the patterns noted above, plus other patterns such as amphi-Atlantic distributions in forms having no obvious means of dispersal. Patchiness, disjunctions, and latitudinal and longitudinal ranges are also very important, but above all there are the areas of endemism. Indications from the fossil record are also plotted if appropriate. The patterns observed can then be checked against available hypotheses for Southern Hemisphere endemism; namely, origin, migration, Gondwanan and Tethyan relictions, and amphitropicality.

What little evidence there is, such as one important fossil locality for the brachyuran *Cancer* (Miocene of Java) or two extant localities for the cephalocarid, *Hutchinsoniella*, is often taken at face value. This is certainly open to criticism but the conclusions drawn are generally falsifiable. Therefore, as long as the pitfalls are known, there is no harm in this approach since it appears to be capable of generating testable hypotheses having predictive value (Ball, 1975).

CRUSTACEAN DISTRIBUTIONS

Abele's (1982) discussion of the biogeography of Crustacea includes some aspects of paleogeography, patterns of species richness, migrations and morphology. It also provides distributional information on the Cephalocarida, Branchiopoda, Remipedia, Ostracoda, Mystacocarida, Branchiura, Copepoda, Cirripedia, Leptostraca, Hoplocarida, Syncarida, Pancarida (Thermosbaenacea), Mysidacea, Cumacea, Spelaeogriphacea, Amphipoda, Isopoda, Tanaidacea, Euphausiacea, Amphionidacea and some Decapoda. This informative material includes biological aspects such as habitat requirements, life history and dispersal capabilities. However, the single distributional chart given includes the Cephalocarida, Anaspidacea, Spelaeogriphacea, Mystacocarida, and Pancarida (Thermosbaenacea); a montage that is not particularly informative. Schram (1986) adds to this background, in good part by plotting the distributions of a number of crustaceans on separate charts, some of which illustrate amphitropicality and/or Southern Hemisphere endemism. While both authors note the classical freshwater relicts of Gondwanaland such as Anaspidacea, Parastacidae and Phreatoicidea, neither notes Southern Hemisphere endemism among marine forms.

RELICTS AND RELICS OF GONDWANALAND

Since Gondwanan distributions should be relatively easy to identify, and since this paper is primarily involved with the origin of Southern Hemisphere endemism among the crustaceans, some apparent Gondwanan examples will be given first. Abele (1982) reviews the situation for the branchiopods and argues that while passive dispersal may occur, the distribution of genera may be more the result of continental movements. Likewise, Tasch (1987) concludes that the distribution of conchostracans between the five Gondwanan continents was by nonmarine dispersal in the Palaeozoic or Mesozoic.

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[3] The term 'paramphitropical' identifies transtropical species, genera or even higher taxa that show preferences (relative abundance, condition, habitat, emergence etc.) for the higher portions of their latitudinal range (Newman and Foster, 1987; see *Lyreidus tridentatus* in the West Pacific, and *Cancer* in the East Pacific and elsewhere at bathyal depths in the tropics, in the following discussion).

These findings do not preclude long-range dispersal, but if it is taking place now it is not particularly evident. Much the same has been said for other fresh water groups; the branchiuran genus *Dolops*, the phreatocid isopods, parastacoid astacurans, and anaspidaceans. According to Abele (1982), *Dolops* only occurs in Tasmania, South America and Africa, but it is parasitic on freshwater fishes whose distribution is beyond the scope of the present paper. Perhaps the strongest cases can be made for the phreatoicids (Fig. 6A; India, Australia, Tasmania, New Zealand, and Africa but, curiously, not South America), and parastacids (Australia and New Guinea, Tasmania, New Zealand, South America, and Madagascar but not Africa or India) (Williams, 1974; Holthuis, 1986).

The anaspidaceans apparently descended from the Palaeocaridacea, marine forms present in both the Northern and Southern Hemispheres from the Carboniferous into the Permian (Europe, North and South America; Schram, 1986). Since fossil anaspidaceans are known from only the Triassic and Cretaceous of Australia, we are left with the conclusion that they evolved there from marine forms. Gondwana was essentially intact at the time and therefore the occurrence of stygocaridids in New Zealand and South America as well as mainland Australia is consistent with the hypothesis.

It should be noted however that a rather well developed nauplius is passed through in the egg of *Anaspides tasmaniae*. This suggests that anaspidaceans are not too far removed from having had larval stages and, judging from other malacostracans, this indicates that they are not too far removed from the marine environment. Therefore it is possible that the occurrence of stygocaridids in New Zealand and South America in addition to Australia is a West Wind Drift distribution (WWDD; Fell, 1962) rather than a Gondwanaland pattern per se. This is much the explanation given by Feldmann (1986) for the eaglid decapods of fresh waters in southwestern South America, except that their apparent ancestor went extinct in New Zealand.

RELICTS AND RELICS OF TETHYS

Molluscs were used above in exploring Indo-West Pacific and southwestern Pacific endemism because their past distributions were well documented in the fossil record. All were Tethyan, yet some remained tropical while others, probably having had an amphitropical component, became Southern Hemisphere endemics.

There are numerous crustaceans that appear to be Tethyan relicts, but the degree to which these are documented by the fossil record varies considerably. There are some caridean shrimp, including *Procaris*, that are relicts without a fossil record. They are particularly interesting because they are largely restricted to refugial hypogeal and anchialine habitats and then frequently on oceanic islands of the Atlantic and Indo-West Pacific Oceans (Abele, 1982; Maciolek, 1983; Hart *et al.*, 1985; Schram, 1986).

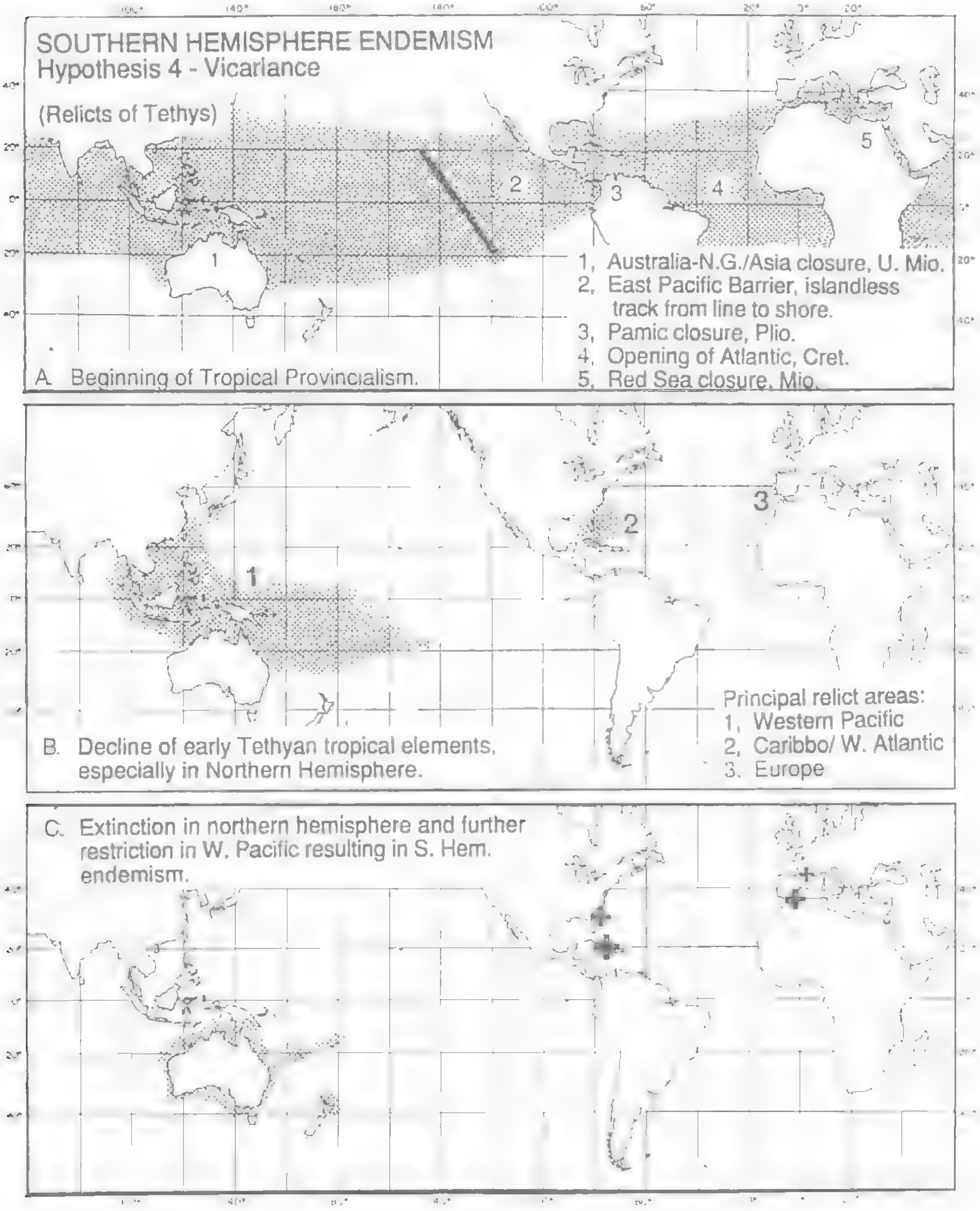
The refugial aspect of oceanic island cannot be over emphasized, as illustrated by the distribution of some other shallow water crustaceans of the Indo-Pacific and Atlantic; namely, the acorn barnacle *Tesseropora* (Oligocene–Recent) and a species each of the burrowing barnacles (Devonian–Recent) *Lithoglyptes* and *Kochlorine* (Newman and Ross, 1977; Schram, 1986, respectively). Both of these groups are more restricted in the Atlantic than in the Indo-Pacific, so that if reliction continues one might expect the Atlantic populations would go extinct first.

While there is evidently a greater diversity of Tethyan relicts in the Indo-Pacific than in the

FIG. 4. Hypothesis 3 — Vicariance. Deep tropical relicts and relics of Tethys. A, Contemporary configuration of the world with the approximate limits of the tropical belt (stippled). Barriers to transtropical dispersal that led to the tropical provincialism we see today include: 1, the Australian-New Guinea/southeast Asia closure (Upper Miocene) blocking equatorial currents between the Pacific and Indian Oceans; 2, the East Pacific Barrier or islandless track between the black bar and the Americas, 3, the Panamic closure (Pliocene) separating the East Pacific from the western Atlantic; 4, the opening up of the Atlantic (cf. Fig. 3); and 5, the closure at Suez (Miocene). B, Decline of Tethyan tropical elements concomitant with cooling at the poles and warming of the tropics, the latter beginning in the Miocene (Shackleton 1984) and the former culminating in the Pleistocene. Principal relict areas initially in: 1, the West Pacific; and 2, the western Atlantic, but also 3, in Europe/North Africa apparently due to the Gulf Stream. Deep tropical elements belonging to this class had pretty much gone extinct in the East Pacific and most of the eastern Atlantic, concomitant with the loss of coral reefs there (Newell, 1971), C, Further decline of this class of relicts included extinction in the Northern Hemisphere and much of the Southern Hemisphere, except for the Indo-West Pacific. Of particular interest here are West Pacific endemics, some of which became restricted to the southwest Pacific as Southern Hemisphere endemics.

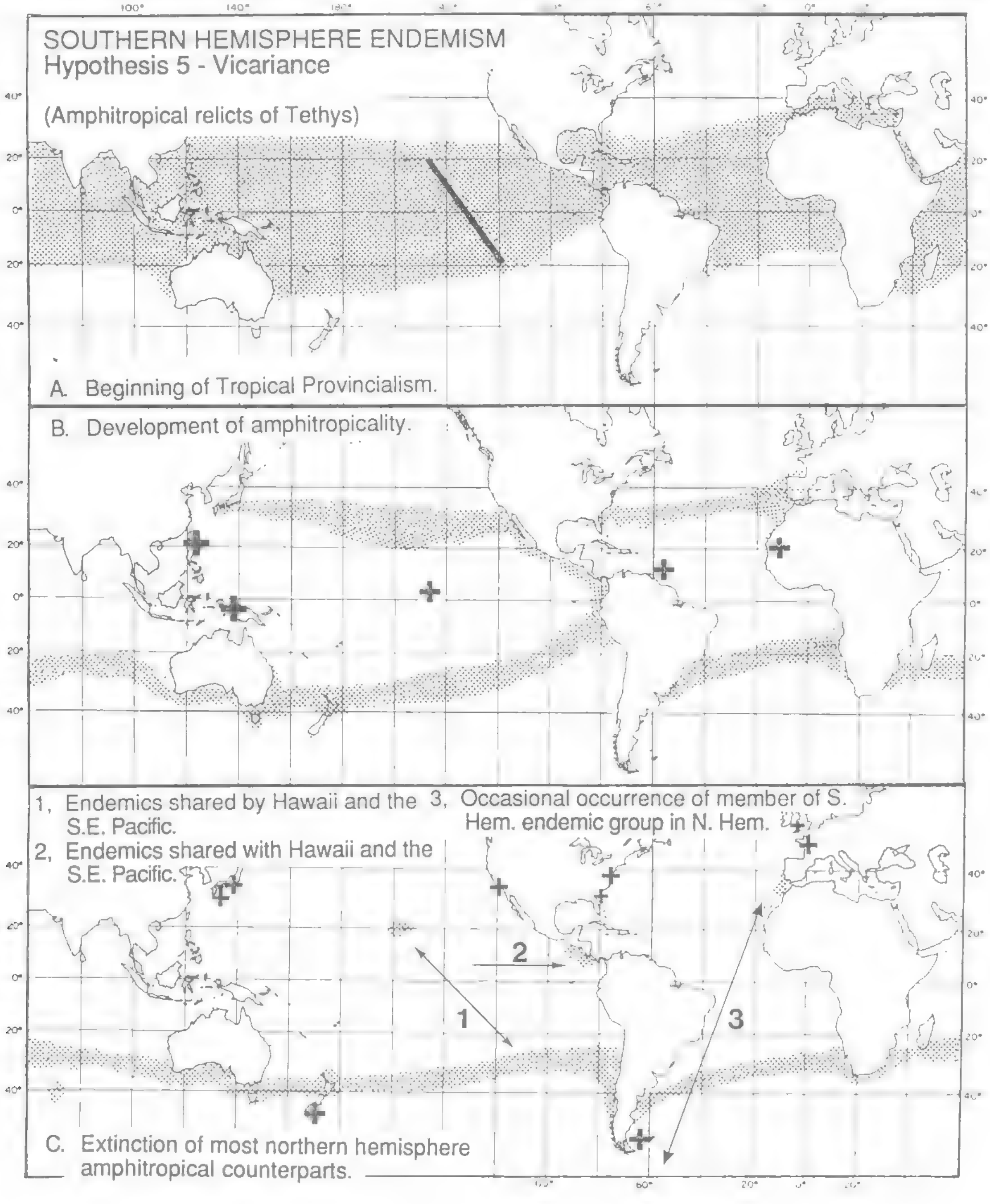
Atlantic, there are some crustaceans at high taxonomic levels that appear to be endemic to the Atlantic; namely, the Remipedia, Pancarida, Spelaeogriphacea, and the Mystacocarida (Pancarida and Mystacocarida have recently been discovered elsewhere). These groups are restricted to anchialine, brackish, fresh water hypogeal and marine interstitial refugial habitats. Unlike the shrimp just noted, they are blind and otherwise have life histories that are apparently not conducive to long range dispersal.

The Remipedia, known from the Caribbean and allied to *Tesnusocaris* from the middle Car-



boniferous of Texas at the time of Abele (1982), have since turned up on the opposite side of the Atlantic, in the Canary Is. (Schram, 1986, fig. 3-3; Schram *et al.*, 1986, fig. 39). Likewise, the Spelaeogriphacea, known to Abele (1982) from freshwater caves in South Africa and from the Carboniferous of Canada, is now known from freshwater in Brazil (Pires, 1987).

Pancarids were originally known from various ground waters around the Mediterranean, from anchialine situations in the Caribbean, and freshwater caves in Texas (Stock, 1976; Bowman and Iliffe, 1988; Schram, 1986, fig. 17-3). Abele (1982) summarises the explanation of Stock (1976) and previous authors for their amphi-Atlantic distribution; namely, Tethyan relicts 'stranded' in-



land by changes in sea level during the Miocene. But it needs to be recalled that the Miocene Atlantic was nearly as wide as it is today, and Schram (1986), citing Macquire (1965), favors plate tectonics as the vicariant event. Pancarids co-occur with remipeds in the Caribbean (Bowman and Iliffe, 1988) which also occur on both sides of the Atlantic, as does one species of cephalocarid to be taken up below and the spelaeogriphaceans in fresh water noted above. Thus, the situation for pancarids is evidently better explained by a tendency to enter ground water and other refugia prior to the opening up of the Atlantic. This is especially attractive when it is noted the Texas locality appears to be on the edge of the Mississippian embayment. That there are in some respects more primitive representatives in marine situations in the Caribbean (Bowman and Iliffe, 1988) is not at all incompatible with an explanation involving reliction via opening up of the Atlantic unless one is willing to speculate that *Monodella* evolved independently on both sides.

Schram (1986) noted that the distribution of pancarids was congruent with that of certain copepods, mysids, isopods and amphipods on both sides of the Atlantic, and that representatives of the last were also known from the Indo-Pacific. Thus, these groups are Tethyan relicts. That the Pancarida was also in fact once a wide-ranging Tethyan group was recently revealed by the discovery of a species in Cambodia (Cals and Boutin, 1985).

Until recently, the mystacocarids presented an enigma to me because they could be envisaged either as having extended their range from the Atlantic around the southern ends of South America and South Africa into the southern extremes of the Indo-Pacific since the Cretaceous (Schram, 1986, fig. 34-4, a centre of origin hypothesis), or as having been excluded from oceans of the world except the Atlantic. The latter, a reliction hypothesis, received some support in the fact that their present distribution is apparently amphitropical and that the South American species belong to a distinct genus, *Ctenocheilocaris* (Hessler, 1988), whereby diversity is greater in the Southern than in the Northern Hemisphere. Since this symposium, R.R. Hessler has shown me a photomicrograph of a mystacocarid B. Knott sent from Western Australia. Therefore, as far as the present pattern is concerned, the centre of origin hypothesis has been falsified. But, as with virtually all groups, we still do not know when or where the mystacocarids originated.

AMPHITROPICAL DISTRIBUTIONS

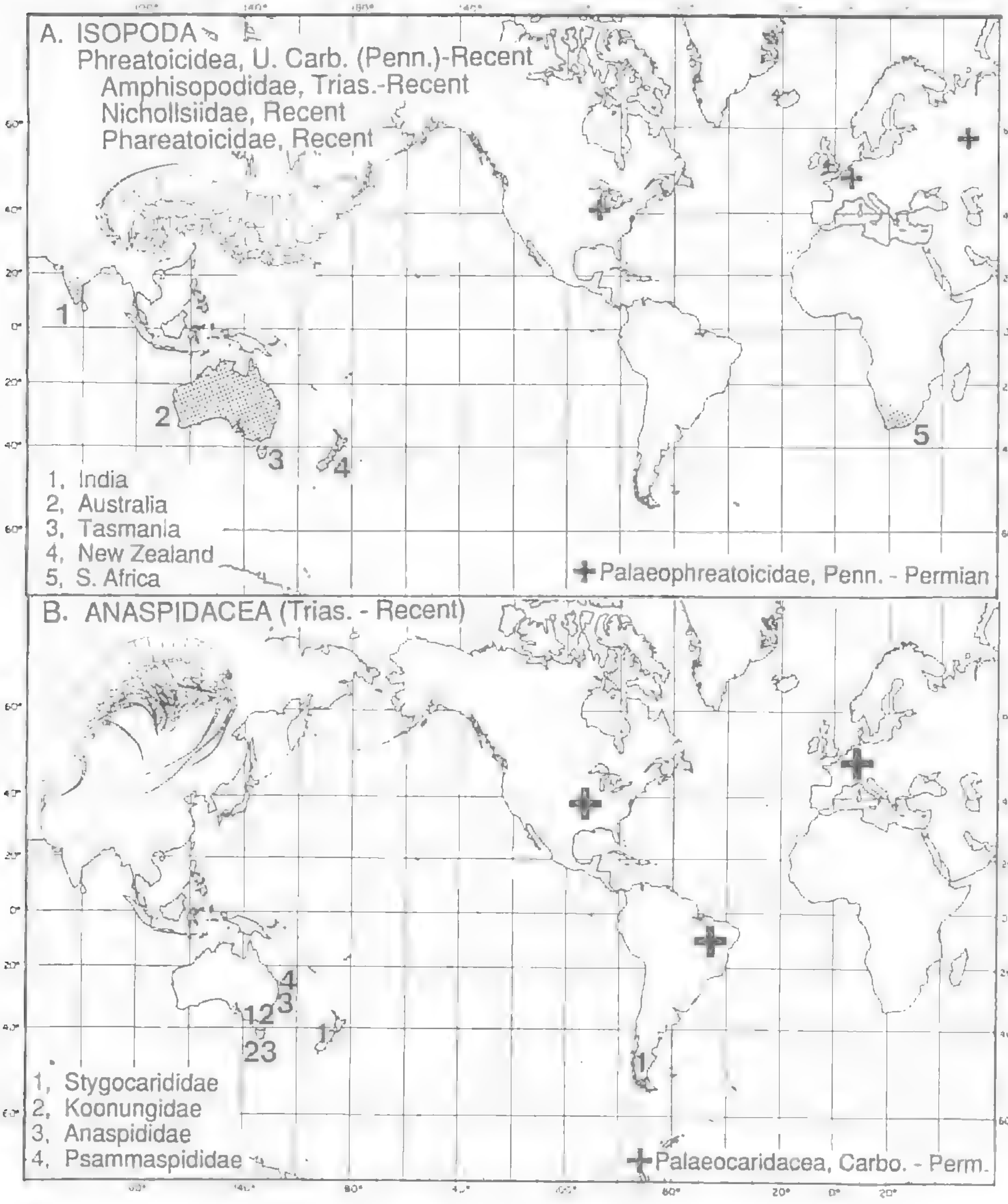
Schram (1986) plots a number of distributional patterns, several of which, including that for the mystacocarids just noted, can be observed to have an amphitropical component. One involves the bathysquillid hoplocarids which apparently have Jurassic affinities. They are known from the Caribbean, and also from the Indo-West Pacific where they are amphitropical (Schram, 1986, fig. 5-7). Then there is the asellote isopod, *Nannoniscus*, dubbed by Schram (1986, fig. 12-6) as 'ubiquitous' but actually as far as it is known strongly amphitropical, especially in the Atlantic. Another of this group might include a wood-boring amphipod, *Chelura terebrans*, of the North Atlantic, South Africa, S.E. Australia and New Zealand had it not been inferred that the

FIG. 5. Hypothesis 5 — Vicariance. Amphitropical and paramphitropical relicts and relics of Tethys: A, Contemporary configuration of the world with the approximate limits of the tropical belt (stippled, cf. Fig. 4A for fuller explanation). Tropical forms are not equally steno- or eurytopic, nor do they have identical temperature optima. Consequently there are patterns within such a uniformly stippled area reflecting these and other characteristics, such as substrate or water mass preferences. B, Evolution of advanced, presumably more competitive tropical forms (Théel, 1911), and/or warming of the tropics beginning in the Miocene (Valentine, 1984), excluded many older elements from the central and deep tropics. Thus a distinct class of Tethyan relicts known as paramphi- and amphitropicals was produced (stippling). Paramphitropicals tend to occur under eastern boundary conditions, as indicated by the stippling in the East Pacific. The eastern Atlantic could also be stippled, but examples of paramphitropicality are apparently uncommon there. These patterns can be detected to varying degrees in both oceanic and coastal forms. C, With further reliction, many Northern Hemisphere populations become extinct, whereby their Southern Hemisphere counterparts become endemic. The fact of extinction in the Northern Hemisphere is based on the fossil record, although some quasi Southern Hemisphere endemics (widely distributed populations in the south but with some Northern Hemisphere representation) can be interpreted as belong to this class. Remnants of previous connections with the Northern Hemisphere include 1, endemics shared between Hawaii and the South Pacific, 2, endemics shared with the East Pacific as well as Hawaii and the South Pacific, and 3, endemics having representation elsewhere in the Northern Hemisphere such as in the northeast Atlantic as indicated here (Newman ,1986; Newman and Foster, 1987).

species had been introduced to the Southern Hemisphere (and to California) by ships.

Abele (1982) and Hessler (1984) review and Schram (1986) plots the distribution of cephalocarids (Fig. 7A), but none attempts to analyse the overall pattern. It can be argued the distribution is poorly known and likely too incomplete to allow an analysis. After all, there are but four genera, nine species and about eleven localities in the world to work from. At first glance the pattern may appear little more than random, but on close inspection and the application of biogeographical principles, patterns become evident.

The first cephalocarid genus, *Hutchinsoniella*, was described some 40 years ago. It is still monotypic and known only from the Atlantic where, instructively,



it is amphitropical (Fig. 6A). The second genus, *Lightiella*, discovered in California at about the same time, is now known by two species from the Caribbean and one from New Caledonia (a relatively isolated southern outpost). It is therefore at least Tethyan as well as amphitropical in distribution. Likewise, species of *Sandersiella*, a genus first described from Japan, have turned up on both sides of South America, with that from the east coast (southern Brazil) also occurring on the southwest coast of Africa (Namibia). Thus, not only are all three of these genera apparently amphitropical, two are Tethyan, and the last is amphi-Atlantic (Hessler and Sanders, 1973) at much the same latitudes as the Spelaeogriphacea noted above. And finally, there is the monotypic New Zealand genus *Chiltonella*, whose discovery makes the diversity of cephalocarids greater in the Southern than in the Northern Hemisphere. Along with the species of *Lightiella* from New Caledonia, these taxa have a geographical refugial aspect to their distribution in addition to their minuscule size and habitat.

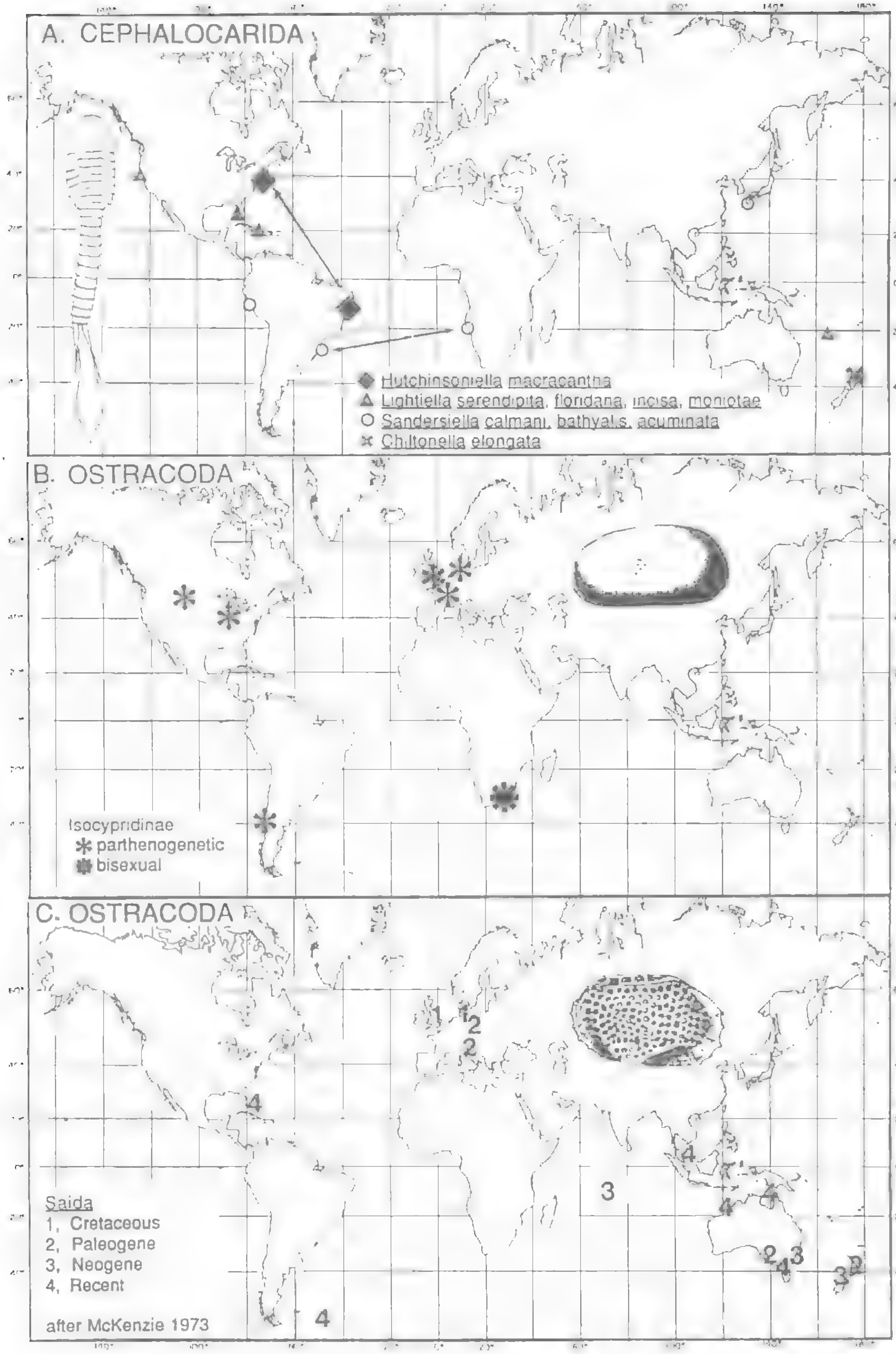
Abele (1982) notes that there has been little local differentiation among cephalocarids and therefore concludes that they are specialists rather than generalists as suggested by Hessler and Sanders (1973). There is no question that they are specialised in size and structure for the refugium afforded by flocculent sediments, and it is probably characteristic of forms so limited, like the mystacocarids in interstitial waters, to show little subsequent diversification. But there is also no question that while specialised, cephalocarids have retained primitive traits known in no other living crustaceans, such as utilising the antennular gnathobases for feeding, multiple ontogeny stages, and second maxillae which are almost indistinguishable from thoracic limbs (cf. Müller and Walossek, 1988). Furthermore, the cephalocarids had to evolve from something not too dissimilar, and there is nothing living from which they can be derived (Hessler and Newman, 1975). In consideration of this and their highly relict geographical distribution, it is clear that the more generalised ancestor of cephalocarids entered this refugium a long time ago (Hessler and Sanders, 1973), likely before the breakup of Pangea and certainly before the breakup of Gondwanaland.

Ostracod biogeography is reviewed by Abele (1882) who cites previous authors who have noted, for example, some freshwater forms with Brazil/West African affinities datable to continental connections during the Early Cretaceous. He goes on to note that arguments for passive dispersal via birds etc. cannot be excluded, as they so readily can for other trans-Atlantic endemics including the species of *Sandersiella* and the spelaeogriphaceans noted above whose amphi-Atlantic aspects could well date back to the same epoch.

Schram (1986) plots two distributions (Fig. 7B, C) displaying amphitropicality, one from the freshwater isocypridine ostracods, the other for the marine genus *Saida*, the latter being the most relevant here. The fossil record for *Saida* begins in the Cretaceous and ends in the Paleogene in northern Europe (Fig. 7C). It also begins in the Cretaceous of Australia where it survives today. Until recently the genus was thought to have gone extinct in the Northern Hemisphere whereby it was considered a Southern Hemisphere endemic. However, there are now (Whatley, pers. comm.) several additional Recent localities known in the world (on the Florida Slope and in the South China and the South Scotia Sea; Fig. 7C). Thus, the genus may presently be paramphitropical. Whatever the case, the example of *Saida* appears to be close to, if not a subset of, Fleming's (1979) observation that much of the marine fauna of New Zealand (and hence at least southeastern Australia) had its roots in northern Europe where it died out in the Miocene.

If it were not for the fossil record, we would

FIG. 6. A, Isopoda, Phreatoicidea, known from four of the six Gondwanan continents including India. While the Phreatoicidae and Nichollsiidae (stippled) are Recent, the Amphisopodidae are known as far back as the Triassic. This is strongly indicative of a Gondwanan distribution, especially since they are freshwater forms. However, their northern hemisphere counterpart, the Palaeophreatoicidae (crosses), are sufficiently old (Pennsylvanian-Permian, Schram, 1986) to make them relicts of Pangean as well. B, Syncarida, Anaspidacea: The distribution of anaspidaceans centers on southeastern Australia, with one of the four families ranging east to New Zealand and southern South America. Known from fresh water as far back as the Triassic, their closest relatives, the Palaeocaridacea (Carboniferous–Permian), are known from marine deposits in North and South America as well as Europe (crosses, Schram, 1986). Like the phreatoicids, conventional wisdom is that anaspidaceans are Gondwanan relicts of Pangea. However, their closest ancestors, the palaeocaridaceans, were marine, and a well developed nauplius is passed through in the egg of at least *Anaspides*. Therefore, the occurrence of one family in New Zealand and South America could have been by West Wind Drift dispersal rather than via the breakup of Gondwanaland.


A. CEPHALOCARIDA
◆ Hutchinsoniella macracantha
△ Lightiella serendipita, floridana, incisa, moniotae
○ Sandersiella calmani, bathyalis, acuminata
⌘ Chiltonella elongata
B. OSTRACODA
Isocypridinae
✱ parthenogenetic
● bisexual
C. OSTRACODA
Saida
1, Cretaceous
2, Paleogene
3, Neogene
4, Recent
after McKenzie 1973
1
1
2
2
4
4
3
4
4
2
4
3
3
2
4

have no way of knowing the long history of *Saida* nor that it may have long had a paramphitropical component. It is examples like this that cause pause in accepting a Southern Hemisphere origin for the anaspidaceans. Further along these lines are two groups of barnacles, acrothoracicans and balanomorphs, once potential candidates for a Southern Hemisphere origin but now also known to be or once to have been amphitropical. Both groups of barnacles have Tethyan representatives in the tropics.

Acrothoracican barnacles are mostly found burrowing in limestone substrates and they range from Devonian to Recent. Schram (1986, fig. 41-3) plotted the distribution of a species each of the generalized lithoglyptid genera *Lithoglyptes* and *Kochlorine*. These were dubbed 'circumtropical', but it can be observed that the two species are not only quite patchily distributed but are almost mutually exclusive; that is, *Lithoglyptes spinatus* occurs in the Caribbean and Indo-West Pacific while *Kochlorine hamata* occurs in the East Pacific, eastern Atlantic and the Indo-Pacific. The patchiness is interesting because it also can be seen from the data on *Cryptophialus*, the more advanced of the two acrothoracican genera in the Cryptophialidae (Tomlinson, 1969; Fig. 8A). Like *Kochlorine*, populations are known from the East Pacific and eastern Atlantic, but in the East Pacific *Cryptophialus* is amphitropical. Then, instructively, there are no records for *Cryptophialus* from the Indian Ocean, except from southern Madagascar; and records from the West Pacific tend to be insular, on or near the Pacific Plate (Fig. 8A)

The second and more primitive genus of the Cryptophialidae, *Australophialus* (Fig. 8B), was until recently known by four species in the Southern Hemisphere, one each from New Zealand and Antarctica, and two in South Africa (Tomlinson, 1969; Newman and Ross, 1971). Like the species of *Cryptophialus*, these are found in shallow water except for a bathyal species in the Antarctica. When *Australophialus* was thought to be austral, it would have been a likely candidate for a Gondwanan origin and distribution. However, a species was recently discovered living at bathyal depths off Gibraltar (Turquier, 1985) whereby *Australophialus* became amphitropical (Newman and Foster, 1987). It could be argued that the Gibraltar species had migrated under equatorial waters from South Africa, but the otherwise relict pattern of the genus suggests that, like *Cryptophialus*, it was once more widely distributed in the world, especially the Northern Hemisphere.

A similar switch in our understanding involves the distribution of the acrothoracican, *Trypetesa*, once the sole representative of the Trypetesidae. However, unlike *Australophialus*, its several species have a relict distribution primarily in the Northern Hemisphere on both sides of the North Pacific and North Atlantic. The species are refugial on two counts; 1, they are only found burrowing in the interior of gastropod shells inhabited by hermit crabs; and 2, primarily in latitudinal transitions zones or ecotones (Newman, 1979b, fig. 10). *Trypetesa* would have been a candidate for Northern Hemisphere endemism until it was discovered that there were representatives (two species and a new genus) in southern Madagascar (Turquier, 1977), a refugial region for other marine as well as terrestrial and freshwater species. Thus, this presumed Northern Hemisphere endemic family became amphitropical.

It is instructive to note that the Acrothoracica is known since the Devonian and is therefore the oldest crustacean group having a fossil record covered herein. Interestingly, the distribution

FIG. 7. A, Cephalocarida (locality data from Hessler,1984). Monotypic *Hutchinsoniella* is amphitropical in the western Atlantic, *Lightiella* and *Sandersiella* are Tethyan and amphitropical in distribution, with *S. bathyalis* being amphi-Atlantic, and monotypic *Chiltonella* a Southern Hemisphere endemic. Hence, the Cephalocarida has a relict Tethyan distribution with pronounced amphitropical character and a greater diversity surviving in the southern than in the northern hemisphere. B, Ostracoda, Isocyprididae (modified from Schram, 1986 after McKenzie, 1973, with deletions from McKenzie, pers. comm.). Isocyprids are freshwater amphitropicals previously thought to have a wider distribution in the southern than in the northern hemisphere. However, the southern Australian representatives have since been removed from the group (McKenzie, pers. comm.). C, Ostracoda, *Saida* (modified from Schram, 1986 after McKenzie,1973, with additions from McKenzie and from Whatley, pers. comm.); a marine, perhaps paramphitropical genus with a fossil record stemming back to the Cretaceous of Europe and Australia and, until recently, thought to be a Southern Hemisphere endemic. Since McKenzie (1973), the genus has turned up in the Paleogene of the southern United States and the Cretaceous of Western Australia (McKenzie, pers. comm.), and from the Recent of the Florida Slope, the South China Sea and the South Scotia Sea from moderately deep to deep water (Whatley, pers. comm.).

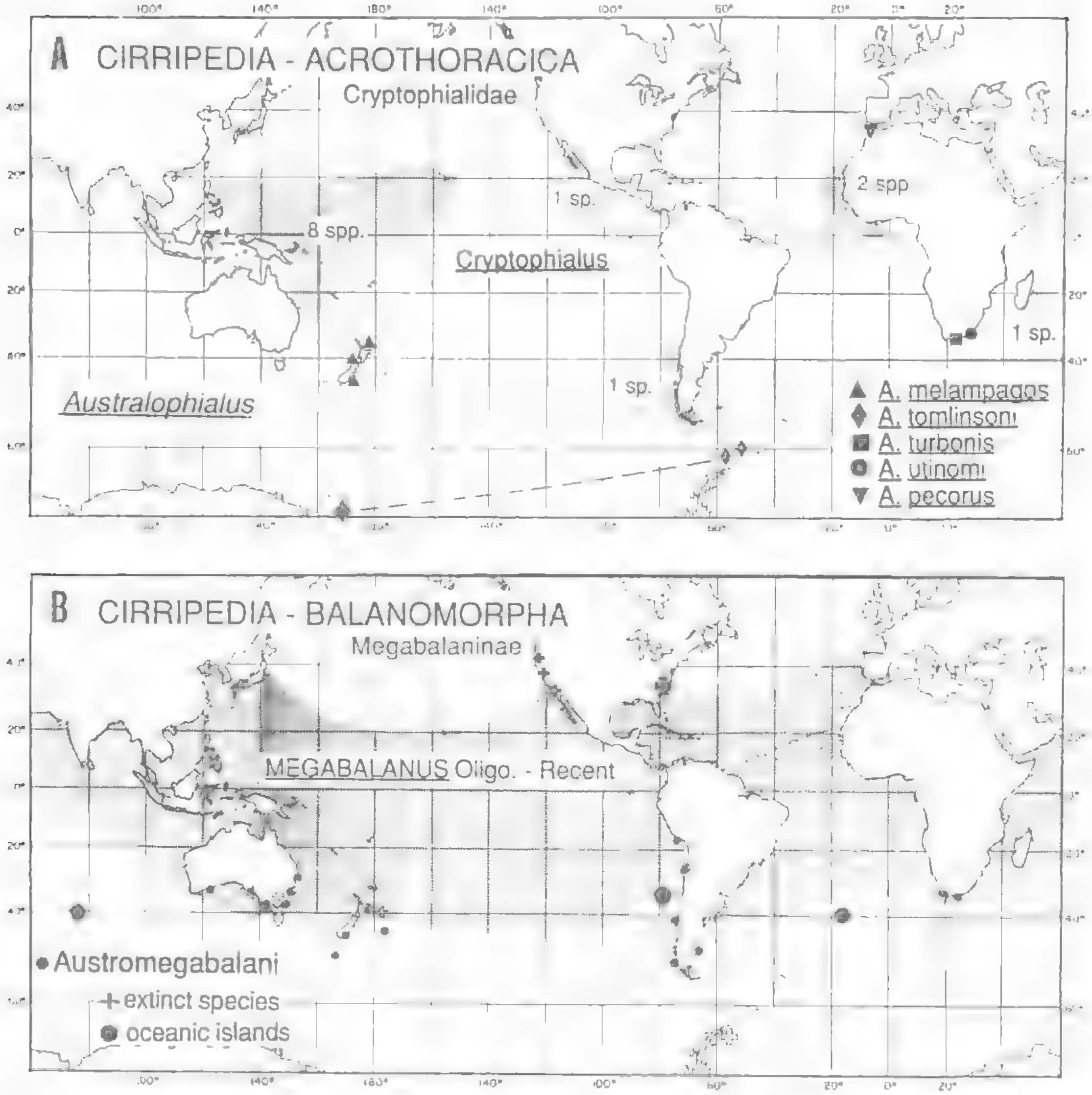


FIG. 8. Cirripedia. A, Acrothoracica, Cryptophialidae. The primarily tropical genus, *Cryptophialus* (stippled), has a distinctly relict Tethyan distribution that is curiously amphitropical in the East Pacific and East Atlantic/Madagascar. The genus *Australophialus* could have been a candidate for a Gondwanan distribution, but recently a species was discovered off Gibraltar, whereby it became an amphitropical rather than a Southern Hemisphere endemic (Newman and Foster, 1987). B, Balanomorpha, Megabalaninae. The advanced tropical genus, *Megabalanus* (stippling), appeared in the Oligocene while the somewhat more primitive Austromegabalani (dots) did not appear until the Miocene in the Southern Hemisphere. The age of the megabalanines as a whole and the occurrence of Austromegabalani on oceanic islands indicated that the latter were not Gondwanan (Newman, 1979a), and the discovery of fossil Austromegabalani on both coasts of North America (crosses) indicated that the Austromegabalani had once been amphitropical (Zullo, 1986; Newman and Foster, 1987).

patterns of shallow-water representatives of all three families have distinct relict characteristics, i.e. patchiness, much regional endemism, and amphitropicality favoring the Southern or the Northern Hemisphere depending on the group.

The balanomorph barnacles first appear in the Upper Cretaceous and the megabalanines appeared in the Oligocene. Several genus-group taxa were recognised as Southern Hemisphere endemics (Newman, 1979a) and one is referred to as the

Austromegabalani here (Fig. 7B). Considering the relatively young age of the subfamily and the occurrence of species of Austromegabalani on oceanic islands of the austral region, it was concluded that they owed their circum-austral distribution to the West Wind Drift rather than to Gondwanaland. Yet, they could have been Southern Hemisphere in origin. It was therefore instructive when it was discovered that the Austromegabalani had once occurred on both coasts of North America (Zullo, 1986; Zullo and Guruswami-Naidu, 1982). Thus it is evident that they were not only Tethyan but were apparently amphitropical.

It is important to note that, as *Austrophialus* is to *Cryptophialus*, the Austromegabalani are more primitive than their tropical counterpart, *Megabalanus*. This fits the Théelian (1911) hypothesis involving replacement in the tropics by advanced forms and the origin of amphitropicality. Competition, predation and other biological factors may have been involved, but warming of the tropics, the amendment to the Théelian hypothesis for the origin of amphitropicality advanced by Valentine (1984), is likely also part of the explanation, especially when one considers the basis for paramphitropical distributions (cf. Newman and Foster, 1987). Now we can look at some other groups, keeping these patterns and apparent trends in mind.

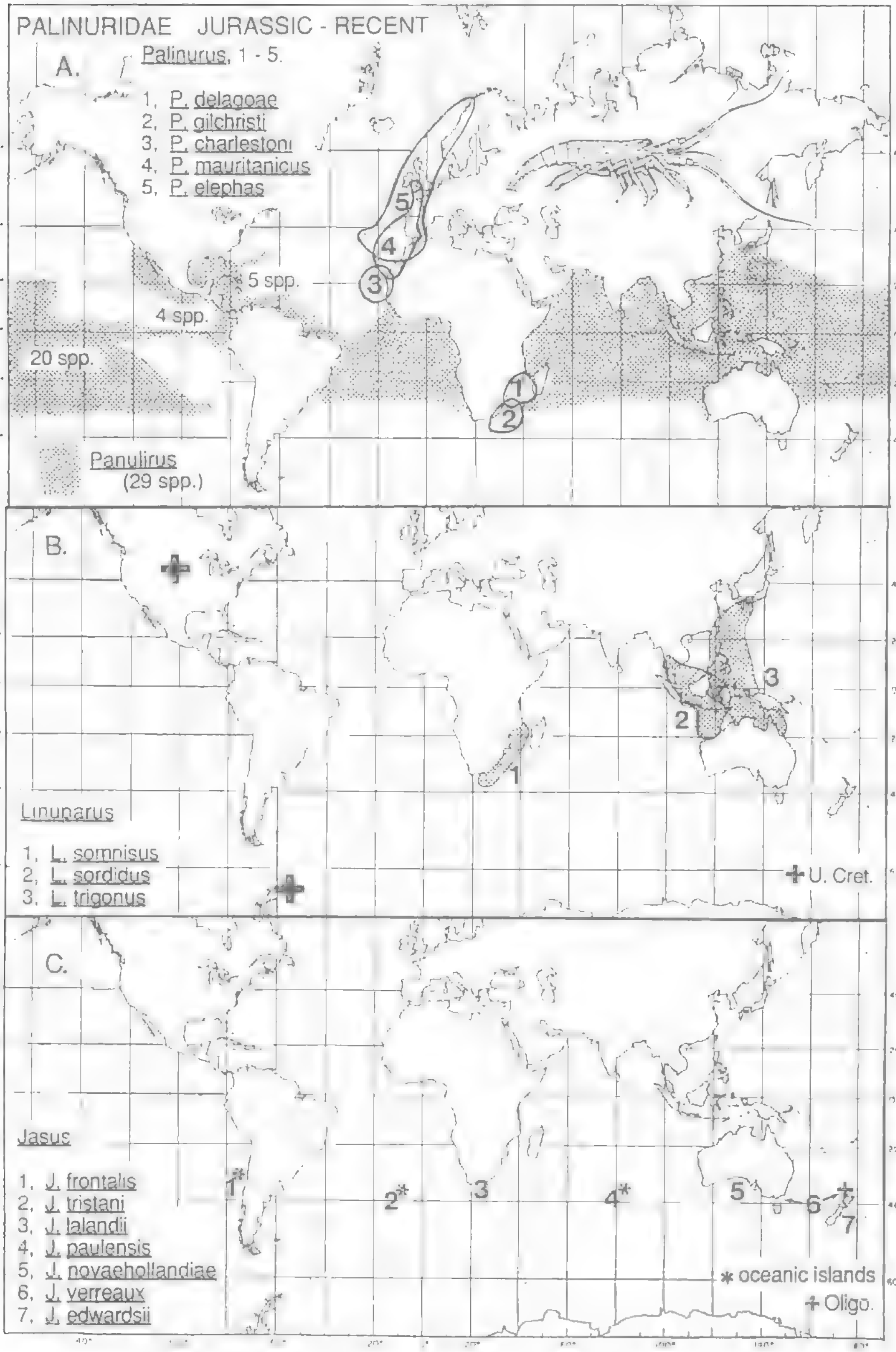
The Palinura, which includes the spiny lobsters and their allies, first appear in the Triassic (Glaessner, 1969). The valuable monograph on the identification of lobster tails (Williams, 1986) also includes a substantial amount of data on current distributions. It was disappointing to find that nothing noteworthy appeared in a preliminary plot of the distribution of genera and species of slipper lobsters (Scyllaridae, Lower Cretaceous–Recent). While diverse in shallow water, the slipper lobsters have a highly derived morphology which likely reduces their interactions on reefs with spiny lobsters to an appreciable extent. Therefore, perhaps unjustly, the details of their distribution will be ignored here.

The spiny lobsters, (Palinuridae, Jurassic) are another matter. The stridulator *Panulirus* (Upper Cretaceous) is well represented in shallow-water tropical waters, there being 24 Indo-Pacific and five tropical Atlantic species (Fig. 9A). On the other hand, another stridulator, *Palinurus*, is represented by five species having a curious distribution in the northeastern Atlantic and southeast Africa (Fig. 9A). It seems prudent to suggest that this amphitropical distribution is the result of reliction rather than migration across the tropics, since a somewhat comparable pattern is known among gastropod molluscs (Gosliner, 1989) as well as the burrowing barnacle *Australophialus* noted above. It is interesting to speculate that if the conditions that have brought about such reliction were to continue, and if species richness and wide ranges are hedges against a taxon's extinction, as with the trypetesid acrothoracicans, one would expect *Palinurus* to become a Northern Hemisphere endemic.

There is another class of reliction among the Palinura, a long recognized example being the Polychelidae; relatively common in shallow water in the Jurassic but now found only at bathy-abyssal depths (Glaessner, 1969). Similarly, the Glypheidae (Triassic–early Tertiary; Greenland, Europe, North America, Australia, New Zealand), were thought extinct since the early Tertiary (Glaessner, 1969) until *Neoglyphus* was discovered at moderate depths in the Philippines (Forest and Saint Laurent, 1981; Forest, Saint Laurent and Chace, 1978). And finally in this category is *Linuparus* which occurred fairly commonly at mid to high latitudes in both hemispheres in the Upper Cretaceous (Bishop and Williams, 1986; Feldmann, 1984, 1988; Feldmann and Tshudy, 1989; Tshudy and Feldmann, 1988), but is presently represented by but three species found at moderate depths; two on the shelf forming the boundary between the Indian and Pacific Oceans and one off southeastern Africa (Fig. 9B).

CENTRES OF ORIGIN

The southern spiny lobster, *Jasus*, a non-stridulator first appearing in the Oligocene of New Zealand, is represented by seven extant species distributed around the Southern Hemisphere (Fig. 9C). They occur on a number of oceanic islands including Tristan da Cunha and Amsterdam/Saint Paul, as well as on the shores of Australia, New Zealand and South Africa (Holthuis and Sivertsen, 1967; Williams, 1986; Pollock, 1990). Taking their Oligocene record at face value and the fact that a good part of their distribution has been via the West Wind Drift (Newman, 1979a), it does seem unlikely that their distribution can be traced back to the breakup of Gondwanaland. Thus we are left with the suggestion that the genus was southern in origin (Pollock, 1990). However, from the foregoing, especially the history of the Austromegabalani which includes two austral groups having much the same distributions as the groups


PALINURIDAE JURASSIC - RECENT
A.
Palinurus, 1 - 5.
1, P. delagoae
2, P. gilchristi
3, P. charlestoni
4, P. mauritanicus
5, P. elephas
5 spp.
4 spp.
20 spp.
1
2
3
4
5
Panulirus
(29 spp.)
B.
Linuparus
1, L. somnisus
2, L. sordidus
3, L. trigonus
1
2
3
U. Cret.
C.
Jasus
1, J. frontalis
2, J. tristani
3, J. lalandii
4, J. paulensis
5, J. novaehollandiae
6, J. verreaux
7, J. edwardsii
1*
2*
3
4*
5
6
7
* oceanic islands
Oligo.

of *Jasus* (Newman, 1979a), and the apparent origin of a brachyuran *Lyreidus* to follow, it would seem equally if not more likely that *Jasus* or its immediate ancestor once had at least a Tethyan if not an amphitropical distribution in the past. While this hypothesis cannot be readily falsified, the alternative (a Southern Hemisphere origin) can be, by virtue of the fossil record.

The ranninid brachyuran, *Lyreidus*, hitherto considered Southern Hemisphere in origin (Feldmann, 1986), appropriately follows here because the alternative hypothesis just noted can be applied. Taking the present distribution at face value, *Lyreidus* appears to be Tethyan (Indo-West Pacific/West Atlantic) and *L. tridentatus* (Hawaii/Japan, one locality off the Philippines and Australia/New Zealand; cf. Feldmann, 1986) may be paramphitropical rather than simply West Pacific. Thus it does not seem that *Lyreidus* was austral in origin. Further suspicion is cast by new fossil evidence indicating that a Tethyan origin with an amphitropical component is likely. Feldmann (1990) has reported on the existence of an ancestral stock, for at least *L. channeri* and *L. nitidus*, from Eocene rocks in both New Zealand *and* the northeast Pacific. Thus the pattern and history appears to be similar to that of *Linuparus* and glypheids, although less severely restricted.

As a final application of the biogeographical principles being used here I would like to analyse the distribution of the brachyuran crab *Cancer* (Fig. 10). The process is instructive because, contrary to previous views, it provides insights into the development of endemism at moderate to high latitudes through reliction rather than radiation. The distribution of *Cancer*, known to Ekman (1935, in 1953), was elaborated upon by MacKay (1943) and Nations (1975, 1979). Nations, who much improved the quality of the taxonomic data base, followed Ekman concerning an inferred North Pacific origin for the genus, and he postulated coastal migration routes about the world to account for the present distribution.

More recently Carvacho (1989) endorsed the biogeography scenario of previous authors, i.e. *Cancer* originated in the Miocene of the North Pacific where most species are found today. Radiation followed: 1, up and over the pole into the Atlantic; 2, down the East Pacific to South America; and hence, 3, to Australia and New Zealand via Antarctica (against the West Wind Drift). However, Nations (1979) was apparently unaware and Carvacho ignored the potential significance of Crosnier's (1976) report of a new species from Madagascar and Reunion I. and Takeda's (1977) records from the Hawaii Islands. The latter relict populations could conceivably be worked into the hypothesis but the former does not fit into a North Pacific origin and radiation hypothesis very well at all. Likewise, records of a cancrid in the Mio-Pliocene of Kerguelen (Richers de Forges, 1977; Noel and Lemaire, 1990) cause further pause. Clearly, as with *Lyreidus* and *Jasus* noted above, a more plausible alternative needs to be explored.

Could the distributional pattern of *Cancer* available to Carvacho have been better explained as the result of reliction than of radiation? In addition to appearing distinctly Tethyan, the pattern reveals other relict elements including: 1, an east–west disjunction in the North Pacific in which one species (*C. amphioelus*) is shared by both regions; 2, an amphitropical pair (*C. porteri* - *C. johngarthi*) displaying low latitude submergence in bridging the gap between hemispheres in the East Pacific (thus making the distribution paramphi- rather than pure amphitropical); 3, a species in South America (*C. polydon*) in the Pliocene of North America and therefore once amphitropical; and, 4, the genus being amphitropical in the Indo-West Pacific, the Southern Hemisphere representatives being in relict areas (southeastern Australia, intro-

FIG. 9. Palinura, Palinuridae (Jurassic; distributional data for extant forms from Williams, 1986). A, The spiny lobster, *Palinurus* (Upper Cretaceous) includes five species, two in southeast Africa and three ranging from North Africa to Norway, an amphitropical distribution with representatives of the widely distributed tropical genus, *Panulirus*, in between. It would appear that *Panulirus* replaced *Palinurus* in the tropics of at least the Atlantic if not the Indian Ocean, the Indo-West Pacific and elsewhere. B, *Linuparus*, widely distributed in shallow water to relatively high latitudes in both hemispheres in the Upper Cretaceous (Bishop and Williams ,1986; Feldmann and Tshudy, 1989), is presently represented in two relict areas by three species in moderately deep water. C, *Jasus* (Oligocene of New Zealand), occurs on oceanic islands as well as continents reached by the West Wind Drift. It therefore occupies a time frame and pattern comparable to that of the Austromegabalani (Fig. 9B) and thus does not likely represent a Gondwanan distribution. *Jasus* has been inferred to have originated in the Australia/New Zealand region (cf. Pollock, 1990) but, considering the relictions of Palinura noted above, and some others noted in the text, an amphitropical Tethyan reliction rather than a southern hemisphere origin and radiation is a distinct possibility.

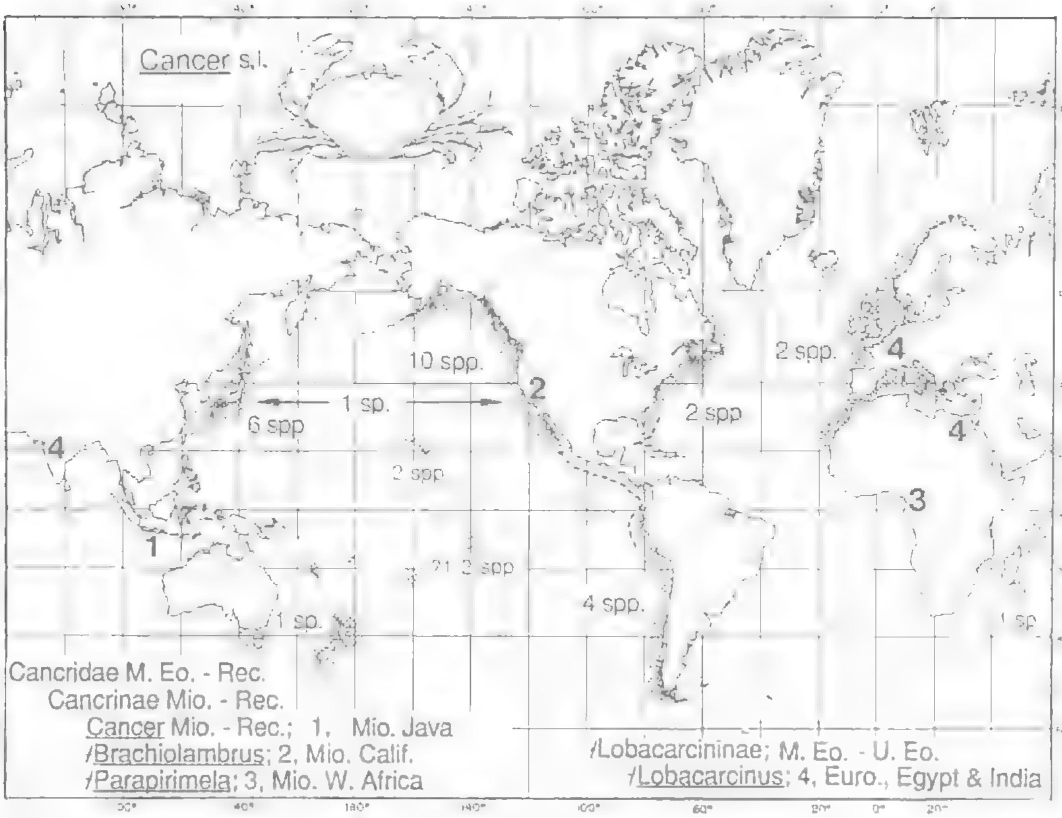


FIG. 10. Cancridae, *Cancer*. There has been a consensus that *Cancer* originated in the North Pacific where most species are found today (Ekman, 1953; Nations, 1979; Carvacho, 1989). But a plot of the present distribution actually appears to be Tethyan, with a strong paramphi- amphitropical component. The present plot includes a deep-water species from Madagascar, Reunion and Seychelles (Crosnier, 1976), Hawaii (Takeda, 1977), Marquesas and Austral Is. (Poupin and Richer de Forges, this volume), and elsewhere in the Pacific including New Caledonia (Davie, pers. comm.).

duced, or perhaps reintroduction from New Zealand [cf. McLay, 1988], and Madagascar).

These facts suggest Tethyan reliction. So does the unique offshore dispersal of outer coast *C. magister* larvae, compared to those of the inland-sea population in British Columbia described by Jamieson and Armstrong (this volume); possibly a relic behavioural pattern related to their once having had more western populations.as far west as northern Japan. This is a testable hypothesis because one species, *C. amphioetus*, presently has relict populations in North America and Asia. Do the larvae of the western populations behave like those of offshore *C. magister*? Yet it can always be argued that the apparently relict distributional aspects are perhaps still compatible with the North Pacific Miocene origin and subsequent radiation hypothesis. Therefore we need to probe the matter a little further.

A look at the fossil record of the Cancridae, of which *Cancer* is the sole surviving genus, reveals some facts that are unreconcilable with the North Pacific origin and radiation hypothesis: 1, *Cancer* itself went extinct in the deep tropics (Java) in the Miocene; 2, *Brachiolambrus* went extinct in the Miocene of California; 3, *Parapirimela* went extinct in the Miocene of West Africa; 4, *Lobacarcinus* (monotypic subfamily Lobacarcininae) went extinct in the upper Eocene of Egypt and India (Glaessner, 1969). Thus the Cancridae had a tropical/subtropical history in the Palaeogene, before the tropics began to narrow in the Oligocene and to warm in the Miocene. These observations, the present paramphitropical distribution, and the relict patterns pointed out above, are not characteristics of a relatively recent radiation but rather reliction of a previously wide ranging Tethyan complex.

There are some unpublished data that also need to be mentioned. A *Cancer* (identified by Crosnier) has recently been taken from deep water in French Polynesia (Marquesas and Austral Is.; Poupin and Richer de Forges, 1990, this volume). Crosnier (pers. comm.) has indicated that the form is very similar to *Cancer guezei* Crosnier from Madagascar, Reunion, and the Seychelles, to a smaller but similar form from Kiribati (= Gilbert Is.), and to *C. sakaii* from Japan. He further notes that this group has a relatively narrow depth range: one record as shallow as 400 m and another as deep as 700 m, but generally between 450 m and 550 m. Knowledge of these relict populations beneath tropical waters on the Pacific Plate in the South Pacific, along with previous knowledge of *Cancer* from Hawaii and off Madagascar, on the Mascarene Plateau, and in the Miocene of Java, is compatible with a Tethyan rather than a North Pacific origin hypothesis.

While the time frame is such that the amphiparamphitropical distribution of *Cancer* developed in response to much the same conditions responsible for the amphitropical distributions noted above in connection with Southern Hemisphere endemism, *Cancer* appears to be doing better in the northern than in the Southern Hemisphere. Other exceptions to the more general trend noted earlier include the Trypetesidae among the barnacles and *Palinurus* among the lobsters. Therefore, while Tethyan reliction, often with an amphitropical component, apparently has generally led to Southern Hemisphere endemism, occasionally it may lead in the opposite direction.

CONCLUSIONS

A number of hypotheses have been explored to explain Southern Hemisphere endemism among the Crustacea. Of the *bona fide* endemics taken into consideration, the phreatocids, parastacids, *Dolops*, and perhaps the anaspidaceans were Gondwanan, while the aeglids and perhaps *Jasus* appear to have had a non-Gondwanan but perhaps southern origin. On the other hand, the ostracod, *Saida*, originally thought endemic to southeast Australia and having a well documented fossil record in northern Europe, is now known to be living in the South Scotia and China Seas, and on the Florida Slope, so that it is perhaps still a Tethyan paramphi- if not amphitropical taxon. Other forms, such as *Lyreidus*, *Australophialus* and the Austromegabalani, were previously candidates for a Southern Hemisphere origin, but they are now known to be or to have been amphitropical.

An amphitropical history in the origin of Southern Hemisphere endemism in some forms leads to the consideration of a variety of other crustaceans (cephalocarids; *Cryptophialus*, the Trypetesidae and other acrothoracicans among the barnacles; and the palinurans and some brachyurans among the decapods) that presently display an amphitropical pattern. Some of these appear on the verge of becoming Southern Hemisphere endemics (*Saida* and *Australophialus*), or vice versa (*Palinurus*, Trypetesidae and the Cancrinae).

What the refugial characteristics are that have led to the preservation of Southern Hemisphere endemics among the marine invertebrates have not to my knowledge been identified. But, as for terrestrial and freshwater forms, they probably involve the relative isolation of Southern Hemisphere outposts from each other as well as from the Northern Hemisphere. However, while some Southern Hemisphere endemics enjoy fairly wide distributions, many marine as well as freshwater and terrestrial endemics are found in relatively discrete areas such as southeastern Australia, southern South America, and the southernmost parts of Africa and India. It seems inescapable, whether Gondwanan or Tethyan in origin, that they have been relegated to these areas by reliction. But this does not explain why they have been spared where they are while going extinct elsewhere. For areas like New Zealand, Madagascar, New Caledonia etc., the additional water barriers are an obvious isolating mechanism, especially for terrestrial and freshwater forms, but what about on the continents? A working hypothesis would seem to be that, in addition to isolation, there are currently ecological parameters that have been operating over comparable periods of time. Southern outposts as defined by a high degree of endemism are generally rather restricted and therefore may represent transition zones between biotic provinces. If so, the endemics would be ecotone species enjoying relief from biological interactions afforded by such refuges (Newman, 1979b; Laguna, 1990).

Relatively few examples from the Crustacea have been given here and I apologize for whatever well documented ones may have been missed. Undoubtedly new discoveries of living and fossil forms will shed light on current problems as well as uncover those yet unrecognised. The process will undoubtedly lead to much refined if not better hypotheses enhancing our understanding of the origin of Southern Hemisphere endemism.

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